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RESPONSES OF THE CARNIVOROUS PINK SPOONLEAF SUNDEW (*DROSER*  
*CAPILLARIS*) TO NITROGEN ADDITION, PHOSPHORUS ADDITION, AND  
SIMULATED FIRE

by  
Karina I. Rodriguez Castillo

A thesis submitted to the faculty of The University of Mississippi in partial fulfillment of  
the requirements of the Sally McDonnell Barksdale Honors College.

Oxford  
May 2021

Approved by

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Advisor: Dr. J. Stephen Brewer

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Reader: Dr. Cliff Ochs

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## DEDICATION

This thesis is dedicated to everyone who has guided and encouraged me throughout my undergraduate years. Thank you to all of my professors and mentors who have pushed me and shaped me to be a better student and leader. As a first-generation student, your support is invaluable to me. Thank you to all of my friends and my family who always believe in me and encourage me to keep pursuing my dreams. I truly appreciate your unconditional love and support.



## ACKNOWLEDGMENTS

I would like to express my sincere gratitude to my thesis advisor Dr. J. Stephen Brewer who guided me through the entire process of my thesis completion. The COVID-19 pandemic did not allow me travel to the field sites, but Dr. Brewer, without any hesitation, set up my experiments for me and took pictures for me to analyze. This thesis truly could not have been successful without his continued guidance and support. Thank you for accepting me into your lab and teaching me about the complexity of carnivorous plants.

I would also like to thank the Hoeksema/Brewer/Zee lab group. Thank you for allowing me to present my research to the group each semester in preparation for my thesis defense. Thank you for your encouragement and your insightful comments and suggestions.

Finally, thank you to the Sally McDonnell Barksdale Honors College for providing the research funds necessary to carry out this project. I sincerely appreciate the community the Honors College has given me in the past four years. Thank you for continually pushing me out of my comfort zone and providing me with meaningful opportunities, such as this thesis, full of growth.

## ABSTRACT

KARINA I. RODRIGUEZ CASTILLO: Responses of the Carnivorous Pink Spoon Leaf Sundew (*Drosera capillaris*) to Nitrogen Addition, Phosphorus Addition, and Simulated Fire

(Under the direction of Dr. J. Stephen Brewer)

This study investigated how the carnivorous plant, *Drosera capillaris* (pink sundew), responded to changes in the resources of its habitat, the fire-prone, nutrient-poor wet savannas. It is of interest to determine what soil nutrient(s), nitrogen or phosphorus, limits the survival and growth of pink sundew, and to what extent, if any, does fire affect the survival and growth of this carnivorous plant. My field experiments had twenty plots with two replicate groups consisting of four pink sundews in each plot. From the fall of 2017 to the fall of 2019, only half of the plots were clipped annually, and there was no clipping in either of the plots in 2020. The clipping of the plots, combined with the removal of clippings and existing leaf litter, was intended to simulate low-intensity surface fires in this system, which cause very little plant mortality but reduce aboveground biomass, reduce leaf litter, and increase the amount of light that reaches the soil surface and the short, flat rosettes of pink sundew. Within each replicate, the pink sundews were assigned one of four treatments to measure how the nutrients affected survival and relative growth rate. In a second experiment, ash was also added to half of the control plants with and without simulated fire in one of the sites to determine whether there was another nutrient that benefits the survival or growth of the pink sundews. Relative growth rate (RGR) was quantified by measuring change in rosette area, which was estimated from digital photographs and calculating the area of polygons drawn

around the rosettes using SketchAndCalc. Statistical analyses of survival and RGR were done using R. Results suggested that nitrogen possibly does not limit survival or growth, and additional nitrogen supplied to the soil may actually be harmful. Simulated fire (clipping and litter removal) did not increase the survival or growth of the pink sundews at these sites in the first half of the growing season, despite the fact that fires were previously shown to be important in promoting the emergence and seedling recruitment from a seed bank; however, simulated fire increased RGR of plants in the latter half of the growing season. In addition, there appeared to be an extra benefit of adding phosphorus earlier in the growing season on growth later in the growing season, but only when combined with simulated fire. It is still unclear whether phosphorus is the main nutrient in the ash that is responsible for stimulating the growth when combined with increased light after a fire. These results suggest that nutrients in ash added to the soil (including but not necessarily limited to phosphorus), when combined with increased light associated with fire, increase growth in the carnivorous plant studied here.

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## ***1. Introduction***

Carnivory in plants is thought to be an adaptation to nutrient-poor soils; however, the effect of specific changes in soil nutrients and their interaction with other resources (e.g., light) are not yet completely understood. Noncarnivorous plants obtain nutrients from the soil through their roots, but carnivorous plants use their leaves to capture and digest prey to supplement these nutrients that are usually obtained from the soil (Darwin, 1875). These plants actively attract prey for the purpose of digesting them and absorbing their nutrients (Givnish, 1989).

Most carnivorous plants are associated with sunny habitats with wet and nutrient-poor soils (Givnish et al. 1984; Brewer and Schlauer 2018). Givnish et al. (1984) proposed a benefit-to-cost model to explain the advantage of carnivory in plants in relation to the availability of soil nutrients, light, and moisture. The model assumes that photosynthesis increases with increasing internal supply of nutrients such as nitrogen or phosphorus, but only up to a point. In contrast, the model also predicts that the carbon cost of producing carnivorous lures, traps, and digestive enzymes continues to increase within increased carnivory investment. As a result, the net photosynthetic benefit of carnivory is greatest when nutrient availability is at its lowest. Carnivorous plants therefore are predicted to be at a competitive disadvantage to noncarnivorous plants in nutrient-rich soils. In addition, because photosynthesis can also be limited by light and water, the model predicts that the net photosynthetic benefit will be greater in sunny and moist environments than in shady or dry environments.

The association of carnivorous plants with fire-prone habitats has been described as a paradox, because the benefit of carnivory is predicted to decline as soil nutrient levels increase following fire (Givnish, 1989). Givnish states that carnivorous plants may be at a competitive disadvantage compared to non-carnivorous plants whenever fires result in a short-term increase in soil nutrient availability because of the reduced benefit-to-cost ratio of carnivory in nutrient-elevated plants (Givnish, 1989). However, Givnish's paradox "assumes that the nutrients that increase in availability following fire are those also provided by prey" (Abbott and Brewer, 2020). Fires in nutrient-poor savannas are hypothesized to increase soil phosphorus more than soil nitrogen. The volatilization of nitrogen in fires leads to a reduction in nitrogen availability after repeated fires (Christensen, 1977). Therefore, plants might use carnivory to supplement this decline in available nitrogen. Hence if prey are primarily a source of nitrogen and fire increases phosphorus, but not nitrogen, then the association of carnivorous plants with fire-prone habitats is not paradoxical. Additionally, because fires increase light levels, the growth of carnivorous plants may be more strongly nutrient limited after fires than before fires. There is plenty of light available after a fire because the fire essentially burns away the plants and associated leaf litter surrounding the plant, allowing sunlight to be absorbed more directly.

There are two key points that need to be considered to resolve the paradox: "(1) Do the nutrients that increase following fire differ from those provided by prey (Givnish et al., 2018)? (2) Does the reduction in light limitation following fire far exceed any potential short-term reduction in nutrient limitation caused by a fire-mediated increase in soil nutrient availability in a chronically nutrient-poor soil (Givnish et al., 2018)?"

(Abbott and Brewer, 2020). Answering these questions requires examining how fire, shade reduction, nitrogen addition, and addition of fire-released nutrients such as phosphorus interact to influence the growth and/or survival of carnivorous plants (Abbott and Brewer, 2020).

This study investigated how the pink sundew responded to the addition of soil nitrogen and soil phosphorus and simulated fire (clipping plus litter removal). Specifically, using a field experiment, I examined how survival and growth of pink sundew responded to soil nitrogen addition, soil phosphorus addition, simulated fire, alone and combined, in two wet pine savannas. This experiment was followed by a second experiment that examined how addition of ash to the soil, with and without simulated fire, affected relative growth rate. I tested the following hypotheses: 1) survival and growth of pink sundew are more limited by phosphorus than by nitrogen; 2) survival and growth increase in response to simulated fire; and 3) growth increases in response to ash addition combined with simulated fire.



## 2. Methods

### *Experiment Sites*

The carnivorous plant *Drosera capillaris* Poir, commonly known as the pink spoon leaf sundew, or simply pink sundew, grows naturally in fire-prone wet savannas, and it emerges from a seed bank after fire, which likely occurs because of increased light stimulating the seed germination (Brewer 1999; Maliakal et al. 2000).

To determine the effects of nutrients and light limitations on pink sundews, my field experiment took advantage of an ongoing clipping experiment that was established in 2014 in the Sandy Creek and Grand Bay sites in southeastern Mississippi. The Sandy Creek site (30.8834, -88.8983) is located in the Desoto National Forest (in Stone County, Mississippi), and the Grand Bay site (30.4203, -88.3871) is located in the Grand Bay National Wildlife Refuge (in Jackson County, Mississippi). Both of these sites are considered open wet pine savannas, containing poorly drained, low pH soils, and they have both been historically maintained by regular fires (Abbott and Brewer, 2020). However, the Sandy Creek site is wetter and has lower dominance by bunchgrasses, and more pink sundews are found there (Abbott and Brewer 2020). Both of these sites contain several species of carnivorous plants, including *Sarracenia alata*, *S. purpurea*, *S. psittacina*, *Drosera capillaris*, *D. tracyi*, *Pinguicula lutea*, *P. planifolia*, *Utricularia purpurea*, and *U. subulata* (Abbott and Brewer, 2020).

In 2014, twenty 2m x 2m clipping plots were established at each of these two sites by the thesis advisor, J. S. Brewer. From 2014-2017, all of the plots were clipped annually, but from the fall of 2017 to the fall of 2019, only half of the plots were clipped

annually. The other half of the plots were not clipped since 2017. There was no clipping in either of the plots in 2020, which was the year the experiment concluded. The clipping of the plots, combined with the removal of clippings and existing leaf litter, was intended to simulate low-intensity surface fires in this system, which cause very little plant mortality but reduce aboveground biomass, reduce leaf litter, and increase the amount of light that reaches the soil surface and the short, flat rosettes of pink sundew (Brewer 1999; Figure 1). The lack of clipping in half of the plots starting in the fall of 2017 has allowed the dominant grasses to recover and cast shade at the ground level in these plots.

### *Experiment Setup*

In April of 2020, two groups of four pink sundews were randomly located in each plot. These two groups were given the name replication 1 and replication 2. The only difference between these two groups was their location within each clipping plot. Within each replicate group of four pink sundews, each sundew was randomly assigned a treatment: no nutrients added, nitrogen only added, phosphorus only added, and nitrogen and phosphorus added. An illustration of the experiment setup was shown in Figure 2.

The nutrient treatments were administered by inserting a 0.27 mL slow-release capsule of fertilizer just below the soil surface adjacent to each plant. The nitrogen treatment received Ammonium Nitrate ( $\text{NH}_4\text{NO}_3$ ) (hereafter, N), and its capsule contained 0.22 g of the fertilizer, which contained 0.21 g of  $\text{NH}_4\text{NO}_3$ . The phosphorous treatment received Superphosphate ( $\text{CaH}_4\text{P}_2\text{O}_8$ ) (hereafter, P), and its capsule contained 0.29 g of fertilizer, which contained 0.05 g of  $\text{CaH}_4\text{P}_2\text{O}_8$ . The N + P treatment received

one of each capsule. To distinguish between the different treatments, each plant was marked with a colored flag or nail.

Because there was no beneficial effect of either N or P fertilizer in the first half of the growing season (see Results below) and because ash contains nutrients other than N or P (e.g., potassium, magnesium, manganese), an ash addition treatment was added to the experiment in June 2020 to determine whether pink sundews grew more in the second half of the growing season when clipped and provided with ash. The ash addition treatment was randomly assigned to one of the two replicate control plots with and without simulated fire in each plot at Sandy Creek. There were too few surviving plants at Grand Bay to adequately replicate the ash addition treatments. The ash added was obtained from clippings that were burnt using a barbeque grill, and the clippings were obtained from Sandy Creek. Digital photos were taken in October to assess survival and relative growth rate (RGR) from June to October as a function of ash addition in June, P addition in April, the clipping treatment, and the combination of the ash addition and annual clipping, P addition and annual clipping, and annual clipping alone.

#### *Survival and Relative Growth Rate Analyses*

To determine the RGR and survival of the pink sundews, the responses to treatments presented were recorded at varying times. The treatments were administered in April 2020, and the initial survival evaluation was done in May 2020. Survival evaluations were again done in June for the Sandy Creek site and in July for the Grand Bay site. During evaluations, pictures were taken for later analysis of RGR from April to June for the Sandy Creek site and from April to July for the Grand Bay site. Chi-square

tests of independence were used to determine if the proportion of plants that survived depended on the treatment. Separate analyses were done to compare survival of plants in control and P-addition treatments to survival of those in N-addition and N+P treatments, to compare survival of plants in controls to survival in the P-addition treatment, and survival of plants in N-addition to survival in the N+P treatment. Calculations of chi-square statistics were done using Microsoft Excel.

The pictures were analyzed using the program SketchAndCalc (Dobbs 2011). This program allowed me to trace the irregular border of each pink sundew, and then it automatically calculated the pink sundew's area using a ruler from the picture as reference. With the repeated photos of the plants over the growing season, the RGR in area of each plant was calculated. The growth analyses of the treatment effects on RGR were completed using R, which is a free statistical program used to analyze data. For the first half of the growing season, I used the linear models (lm) function in R to run a three-way analysis of variance (ANOVA) and examined the main effects of N addition, P addition, and the clipping treatment (annual clipping vs. not recently clipped) and their interactions. Because of high mortality in Grand Bay, the growth rate analysis was only done for Sandy Creek. Also, because mortality resulted in several missing values, the three-way ANOVA was done using type II sums of squares, in which main effects were tested first, followed by the two-way interactions and then the three-way interaction.

### 3. Results

When comparing the results of survival for the plants with nitrogen addition at the Grand Bay site, those with the control and phosphorus only treatments had a much higher percentage of plants alive while those with the nitrogen only and nitrogen plus phosphorus treatments had a very small percentage of plants alive ( $X^2 = 49.7$ ;  $p = 1.76 \times 10^{-12}$ ). These results are illustrated in Figure 3 and Figure 4. In a separate analysis, it was concluded that the nitrogen addition with or without phosphorus addition reduced survival, and this was statistically significant based on chi-square tests.

For the Sandy Creek site, there were similar overall results for survival of the plants with nitrogen addition ( $X^2 = 76.6$ ;  $p = 2.10 \times 10^{-18}$ ). However, the plants with the control and phosphorous only treatments had 100% of plants survive, and those with the nitrogen only and the nitrogen plus phosphorous treatments had a greater percentage of dead plants compared to the Grand Bay site. These results are presented in Figure 5 and Figure 6. According to the chi-square tests, there was no significant difference in the survival between the control plants compared to the phosphorous only added plants, nor between the nitrogen only plants compared to the nitrogen plus phosphorous added plants.

For the results of the growth rates of survivors to nitrogen and/or phosphorus addition in the Sandy Creek site, I found that when nitrogen was added, there was negative growth, as indicated by the significant main effect of nitrogen addition in the three-way ANOVA ( $F_{(df=1,71)} = 5.947$ ,  $p = 0.017$ , Figure 7).

When analyzing the results of the survival and growth rate of survivors, in response to clipping and/or phosphorus addition in the Sandy Creek site, I found that

there were actually much fewer pink sundews in the plots that were not recently clipped because of lower recruitment from the seed bank due to more leaf litter and shade; therefore, seedling recruitment may affect the difference in plants dead versus alive. Clipping had no effect on the survival of existing plants, but it did significantly reduce growth, as indicated by the significant main effect of the clipping treatment in the three-way ANOVA ( $F_{(df=1,71)} = 4.322$ ,  $p = 0.041$ , Figure 8). The interaction between clipping treatment and phosphorus addition was not statistically significant ( $F_{(df=1,71)} = 1.616$ ,  $p = 0.208$ ).

In contrast to the first half of the growing season, RGR in the second half of the growing season was significantly greater in the annually clipped plots than in plots that were not recently clipped, as indicated by the significant main effect of clipping treatment in the two-way ANOVA ( $F_{(df=1,35)} = 5.230$ ,  $p = 0.028$ ). However, there was also a trend suggesting that the positive effect of annual clipping on growth late in the growing season depended on whether ash was also added in June or phosphorus was added in April. The clipping treatment x ash/P addition interaction approached statistical significance ( $F_{(df=2,35)} = 2.682$ ,  $p = 0.082$ ). The positive effect of annual clipping appeared to be greatest when combined with ash addition, while there was no beneficial effect of annual clipping when neither ash nor phosphorus was added (Figure 9). The plants showed an intermediate growth response to the combination of annual clipping and P addition (Figure 9). There was no main effect of ash or P addition on growth from June to October ( $F_{(df=2,35)} = 1.007$ ,  $p = 0.376$ ).

#### **4. Discussion**

From these results, I conclude that pink sundews respond poorly to nitrogen addition, both in terms of survival and growth, possibly suggesting that neither survival nor growth is limited by soil nitrogen availability in this species at these sites, but there is not enough evidence to draw the conclusion that nitrogen was not limiting. Sundews may actually get an adequate supply of nitrogen from prey, and additional nitrogen supplied to the soil may be toxic or harmful. Sundews may have also received too much N addition and could have potentially benefitted from less N added. An additional experiment could include looking at the effects of differing amounts of N added to the pink sundew.

Although fires have previously been shown to be important in promoting emergence and seedling recruitment of pink sundews (Brewer 1999, Maliakal et al. 2000), established plants did not show increased survival or growth in response to annual simulated fire (clipping + litter removal) in the early part of the growing season in this study. In fact, sundews responded poorly in terms of growth to annual simulated fire in the early part of the season. Furthermore, phosphorus addition did not improve growth or survival when combined with clipping early in the season. These results suggest that the dramatic increases in densities of pink sundews following fire and subsequent declines with increasing time since fire (Brewer 1999; Hinman and Brewer 2007) are due to increased recruitment after fire, followed by mortality that is unrelated to fire (Brewer 1999). As in the early part of the growing season, survival was not affected by the clipping treatment in the latter part of the growing season.

In contrast to responses early in the growing season, later in the growing season, annual clipping did increase growth rate, especially when combined with ash addition

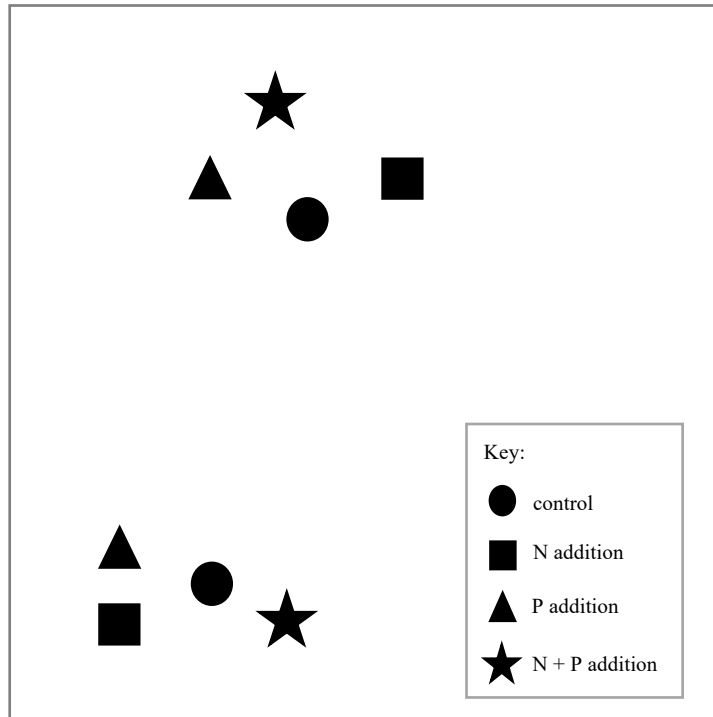
and to a lesser extent phosphorus addition. Therefore, there might be an extra beneficial effect of adding phosphorus earlier in the growing season when combined with clipping. However, this effect is much weaker than the combined effects of annual clipping and ash addition. The results suggest that the growth of established sundews late in the growing season could be increased by fire. However, it remains unclear whether phosphorus is the main nutrient in the ash that is responsible for stimulating growth when combined with increased light after fire. There are potentially other nutrients, such as potassium, magnesium, or manganese, that are found in ash and may be more important to the growth of sundews. Future experiments should examine the combined effects of clipping + litter removal with the addition of these nutrients and compare growth responses to the combined effects of ash addition and clipping + litter removal. That said, an increase in the availability of phosphorus in the soil following fire may in fact still be important, but perhaps it would have a more beneficial effect when added during the peak lightning fire season along the Mississippi Gulf Coast (i.e., May or June; Brewer 2009), as opposed to April.



## 5. Figures



*Figure 1—Photograph of many pink sundews taken by Dr. J. S. Brewer. Image shows how close to the ground the plants are.*



*Figure 2—Diagram of a single plot from the field experiment. This diagram highlights how each of the twenty plots at each site is set up and shows the two replicates that are at each of the plots.*

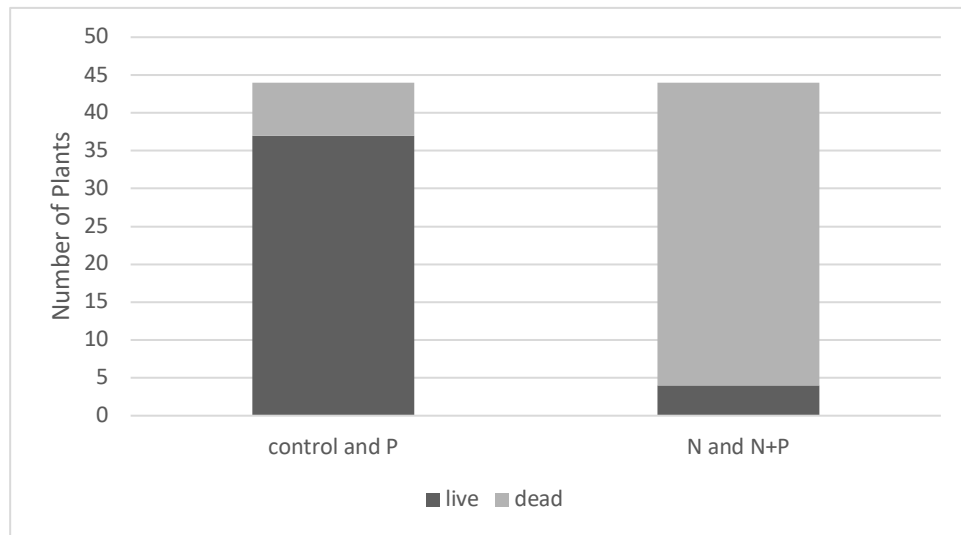


Figure 3—Control and P addition vs. N addition and N + P addition at the Grand Bay site (results as number of plants).

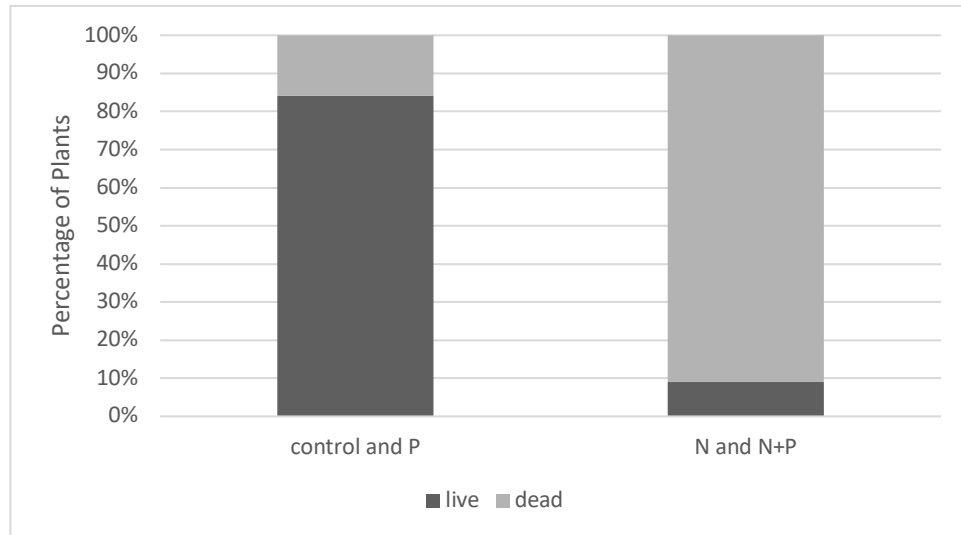
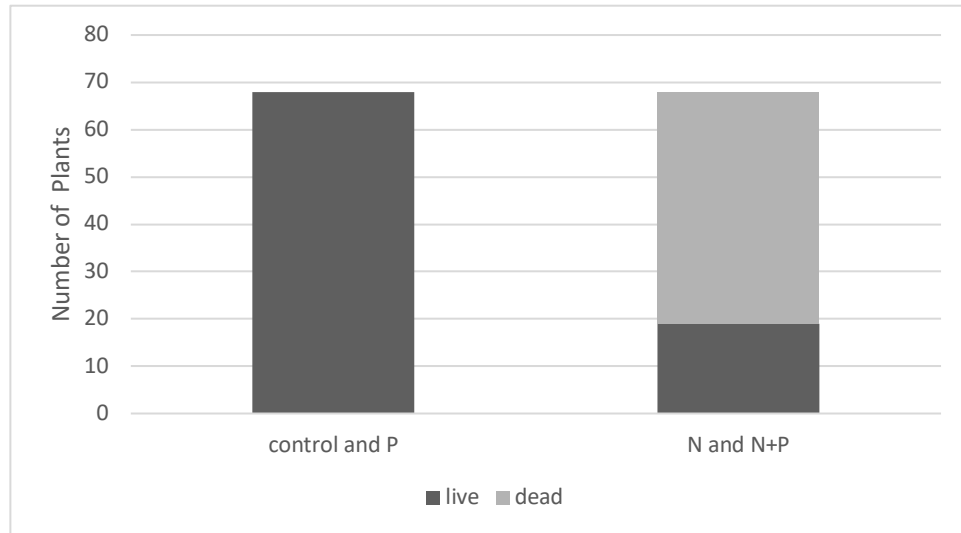
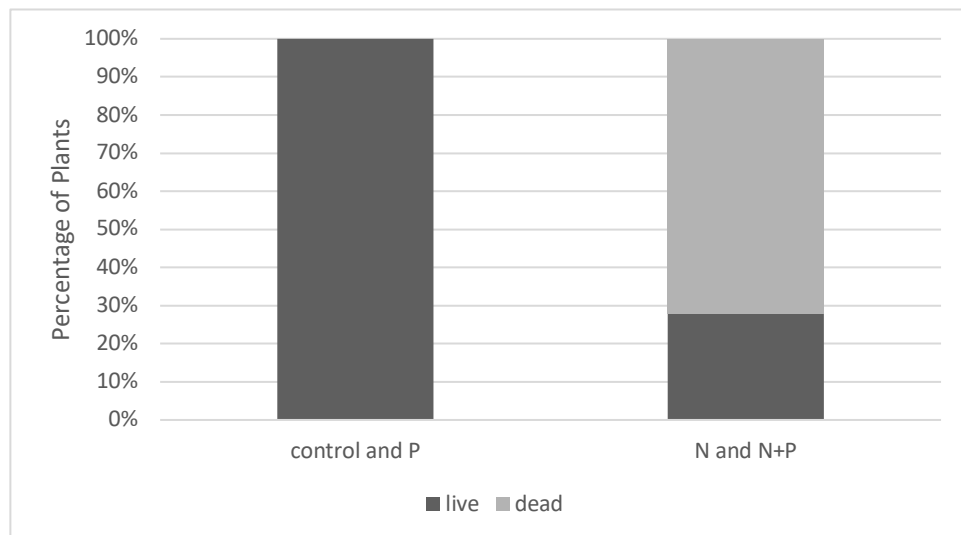


Figure 4—Control and P addition vs. N addition and N+P addition at the Grand Bay site (results as percentage of plants).



*Figure 5—Control and P addition vs. N addition and N+P addition at the Sandy Creek site (results as number of plants).*



*Figure 6—Control and P addition vs. N addition and N+P addition at the Sandy Creek site (results as percentage of plants).*

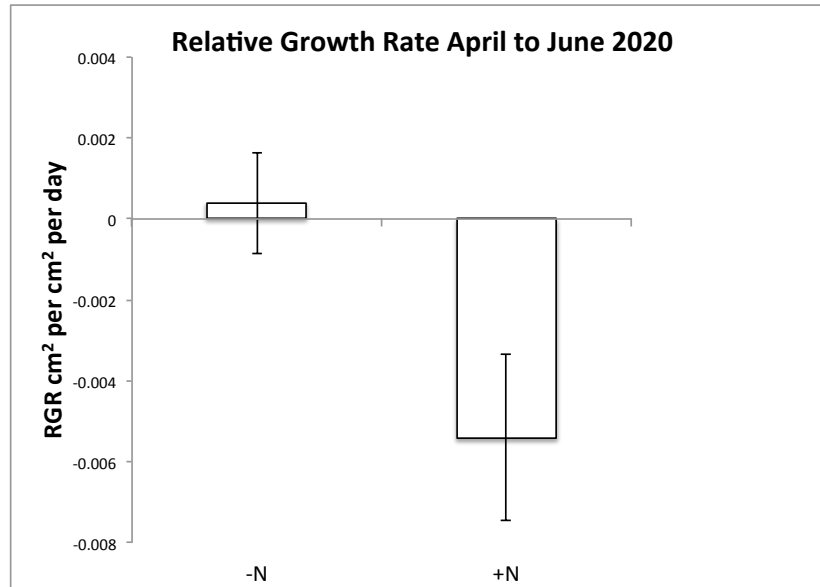


Figure 7—Relative growth rate of N addition vs. no N addition at Sandy Creek. (error bars show standard error)

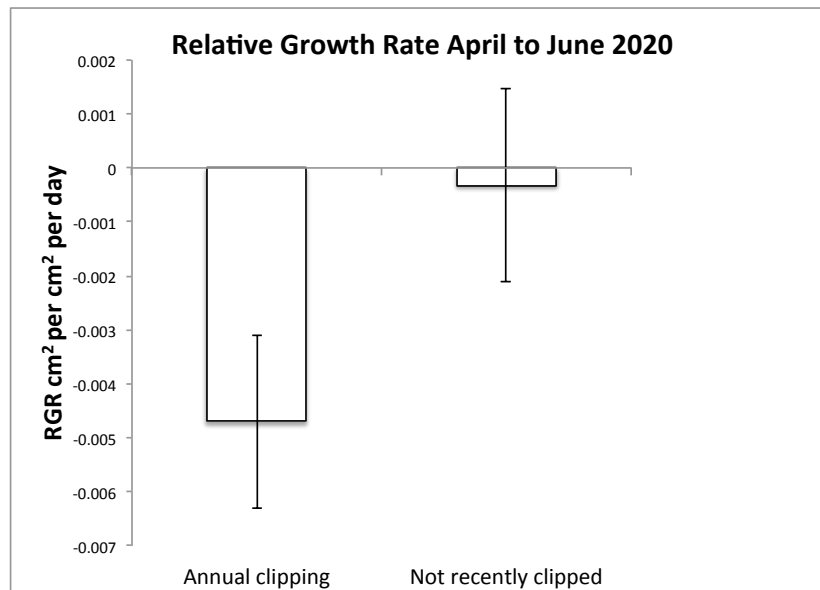


Figure 8—Relative growth rate of annual clipping vs. not recently clipped at Sandy Creek. (error bars show standard error)

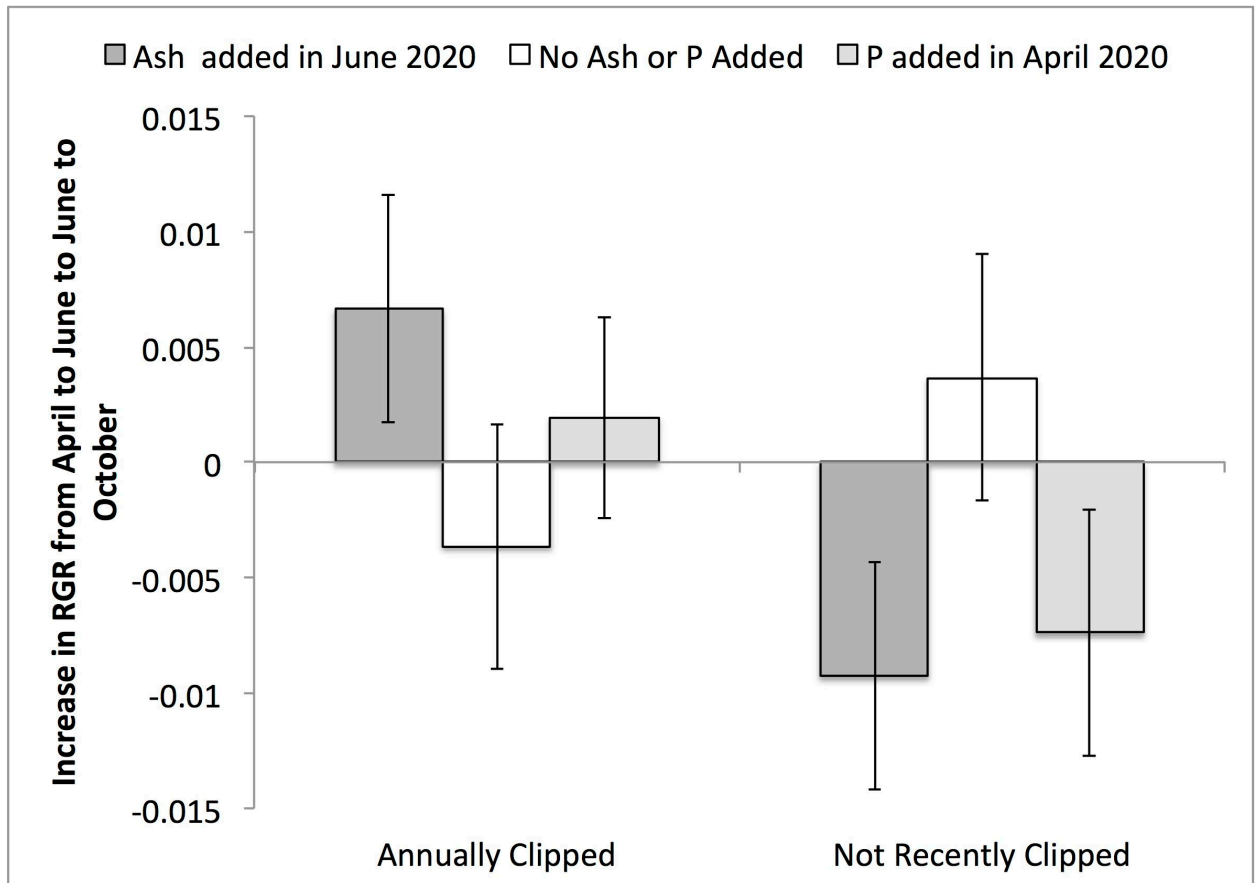


Figure 9— Relative growth rate of ash added vs. no ash or P added vs. P added at Sandy Creek. (error bars show standard error).

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